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CHICAGO JOURNALS

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Source: *The Journal of Geology*, Vol. 77, No. 5 (Sep., 1969), pp. 606-617

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/30062254>

Accessed: 09/10/2013 13:27

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NEW PHYLOGENIES OF THE LOWER ORGANISMS: POSSIBLE RELATION TO ORGANIC DEPOSITS IN PRECAMBRIAN SEDIMENT¹

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ABSTRACT

Classical phylogenies of the lower organisms are based on assumptions recently claimed to be erroneous. Alternative assumptions, more consistent with modern genetic and biochemical data, lead to the construction of new phylogenies. The new phylogenies (one for prokaryote organisms and one for eukaryotes) based on the symbiotic theory of the origin of eukaryotic organelles predict the nature and sequence of organic deposits on the Precambrian earth. Even if incorrect, these phylogenies present a modern framework upon which to compare the many recent reports of organic remains in sediment.

Classical phylogenies of the lower organisms (Klein and Cronquist 1967) are based on certain assumptions which recently have been disputed (Margulis 1968, table 1, left side) and consistent phylogenies for the lower organisms produced on the basis of alternative assumptions (Margulis 1968, table 1, right side). The alternative assumptions, derived from the symbiotic theory of the origin of nucleated cells (Sagan 1967) are based entirely on the results of recent biological work. If, however, the new phylogenies are correct (figs. 1 and 2), they have precise implications, presented in this paper, for the sequence of deposition of organic remains in sediment. Since verification or repudiation by paleontologists and organic geochemists may provide the ultimate arbitration in disputes among microbiologists concerning the evolutionary relationships among the lower organisms, this presentation of the implications for sediment of the new phylogenies was considered in order.

The difference between prokaryotes and eukaryotes (table 1), and not the traditional difference between plants and animals, is now thought to represent the most marked evolutionary discontinuity in living systems

on the earth today (Stanier et al. 1963, chap. 4). On both biological and geological grounds, it seems likely that the microbial prokaryote type of cell evolved and proliferated extensively in the early Precambrian, whereas the eukaryote type of cell apparently did not evolve until the late Precambrian (Schopf 1969). Immense biochemical virtuosity exists in prokaryote microbes which, as a whole, are still probably the most important biological agents of geochemical change (Stanier et al. 1963, chap. 23; Ferguson-Wood 1968, chap. 10). It is highly probable that Precambrian prokaryote activity caused large deviations in the amounts and types of compounds in both the atmosphere and the sediments from those expected on physical and chemical grounds alone. Although all evolutionists agree that prokaryotes are more primitive than eukaryotes, there is no precise agreement concerning the evolutionary sequence (fig. 3, left side; Klein and Cronquist 1967). The symbiotic theory (fig. 3, right side), however, makes the explicit predictions discussed below for organic sediment from the time of the origin of life through the evolution of the lower eukaryotes.

I. THE EARLY PRECAMBRIAN DEPOSITION OF ABIOTIC ORGANIC MATTER

Presumably, most organic materials necessary for continued self-replication in all cells must originally have been produced on

¹ Manuscript received July 5, 1968; revised January 9, 1969.

[JOURNAL OF GEOLOGY, 1969, Vol. 77, p. 606-617]

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PHYLOGENY of the PROKARYOTES
(MONERA KINGDOM)

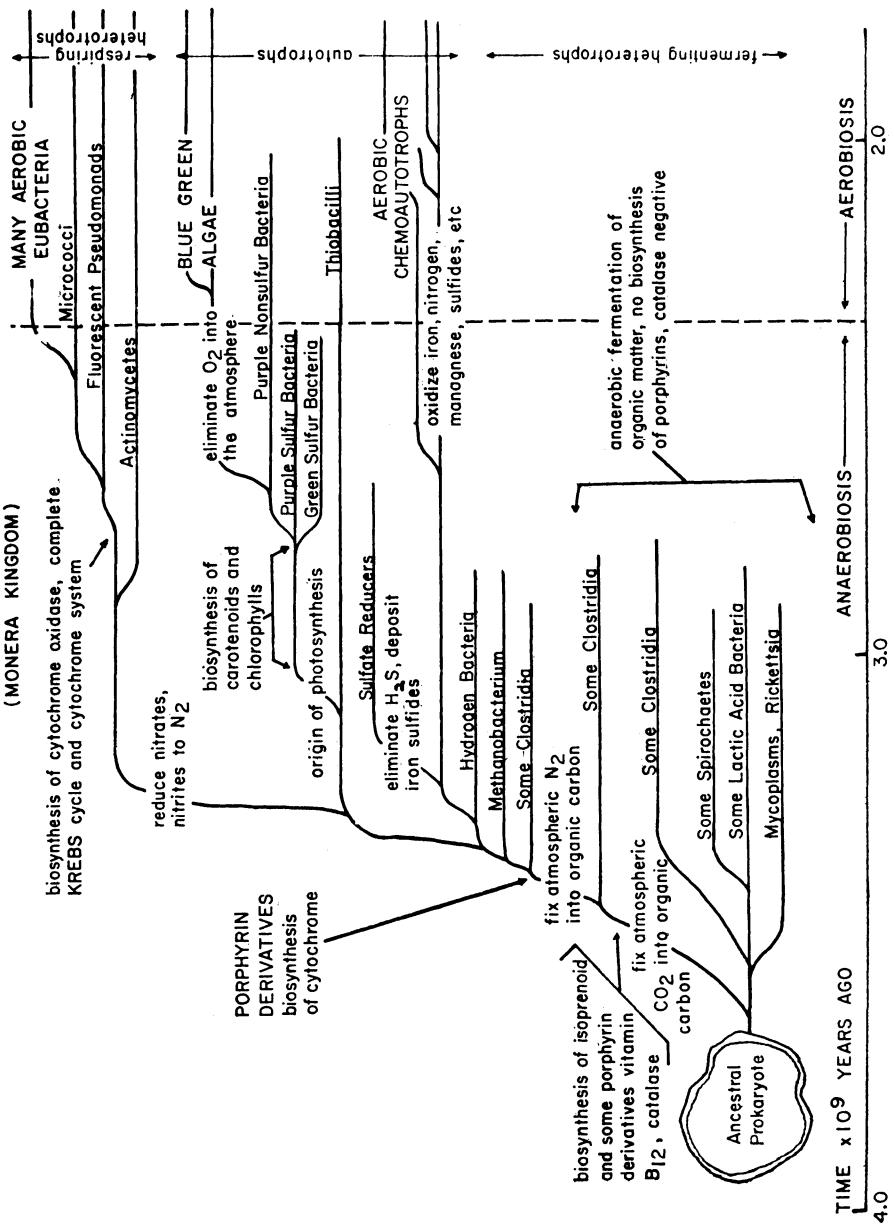


FIG. 1.—Prokaryote phylogeny which forms the basis of the predictions in the text (for additional details see Margulis 1968)

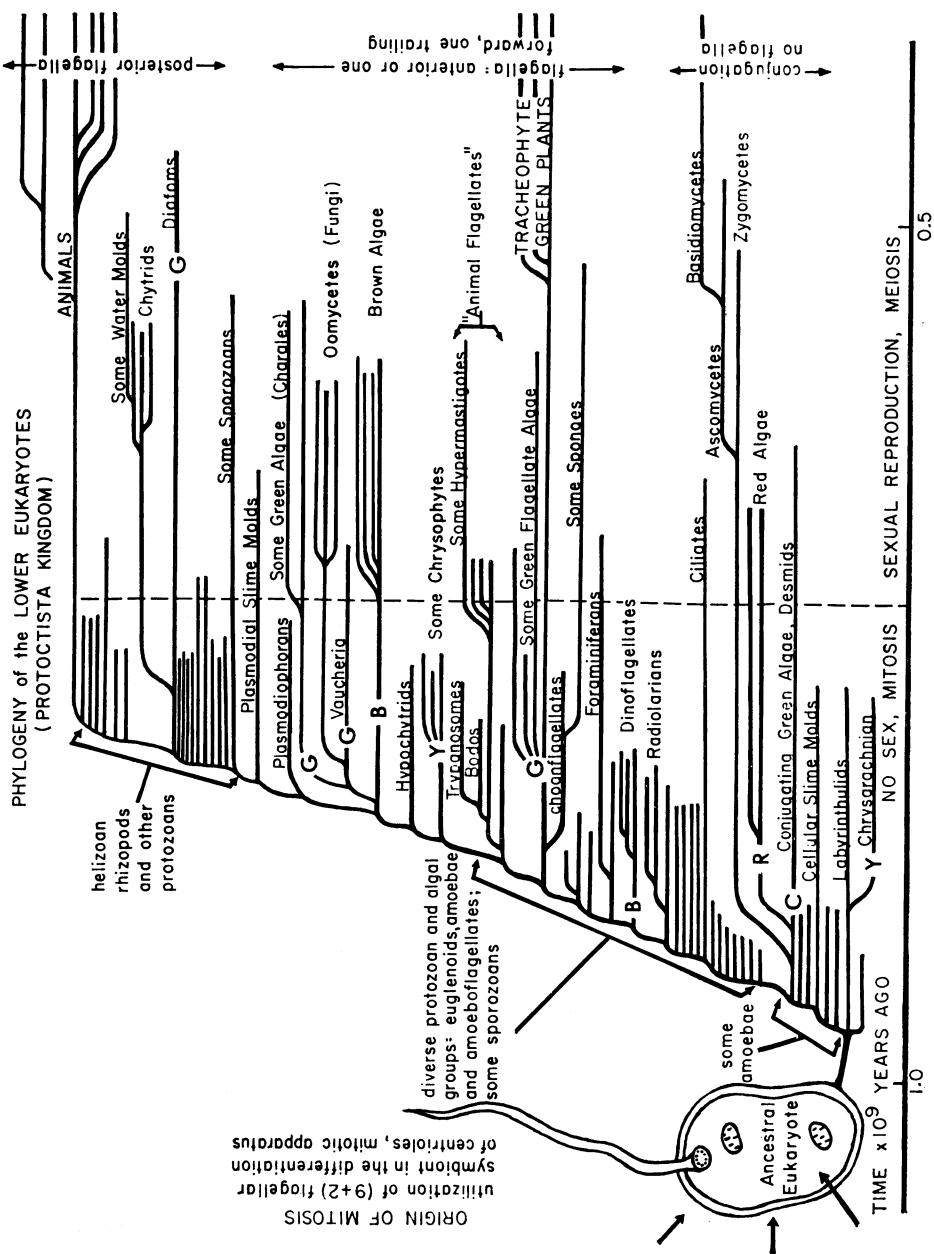


FIG. 2.—Eukaryote phylogeny which forms the basis of the predictions for biogenic organic matter and fossils in the late Precambrian and early Phanerozoic. The letters refer to the predominant pigment colors in the plastids of eukaryotic plants (Y = yellow, R = red, B = brown, G = green). The positions of the letters on the lines indicate the approximate times of acquisition of the photosynthetic plastids by the heterotrophic hosts (see Sagan 1967 for details including the names of the protozoan, fungal, and algal groups indicated).

TABLE 1

A SUMMARY OF THE MAJOR DIFFERENCES BETWEEN PROKARYOTIC AND EUKARYOTIC CELLS

Prokaryotic	Eukaryotic
Mostly small cells ($1\text{--}10\mu$); all microbes; the most morphologically complex are filamentous or mycelial with fruiting bodies	Mostly large cells ($10\text{--}10^6\mu$); some are microbes, most are large organisms; the most morphologically complex are the vertebrates and the flowering plants
Nucleoid, not membrane bound	Membrane-bound nucleus
Cell division direct, mostly by "binary fission," chromatin body which contains DNA and polyamines; does not stain with the Feulgen technique. No centrioles or mitotic spindle	Cell division by classical mitosis; many chromosomes containing DNA, RNA, and proteins; stains bright red with Feulgen technique. Centrioles, mitotic spindle present
Sexual systems absent in most forms; when present, unidirectional transfer of genetic material from donor to host	Sexual systems present in most forms; participation of both partners (male and female) in meiotic production of gametes followed by fertilization
Multicellular organisms never develop from diploid zygotes, show no tissue differentiation	Multicellular organisms develop from diploid zygotes, show extensive tissue differentiation
Includes strict anaerobes (killed by O_2), and facultatively anaerobic, microaerophyllic, and aerobic forms	All forms aerobic (need O_2 to live), exceptions clearly secondary modifications
Enormous variations in the metabolic patterns of the group as a whole; mitochondria absent; enzymes for oxidation of organic molecules bound to cell membrane, i.e., not "packeted"	Same metabolic patterns of oxidation within the group (i.e., Embden-Meyerhof glucose metabolism, Krebs-cycle oxidations, molecular oxygen combines with hydrogens from foodstuffs, catalyzed by cytochromes, water produced); enzymes for oxidation of 3-carbon organic acids within "packeted" membrane-bound sacs (mitochondria)
Simple bacterial flagella, if flagellated	Complex "(9+2)" flagella or cilia, if flagellated or ciliated
If photosynthetic, enzymes for photosynthesis bound to cell membrane (chromatophores); not "packeted" in chloroplasts	If photosynthetic, enzymes for photosynthesis "packeted" in membrane-bound chloroplasts
Anaerobic photosynthesis (does not result in oxygen elimination into the atmosphere [in many members]; photosyntheses may result in the deposition of sulfur or sulfate)	Oxygen-eliminating photosynthesis in all photosynthetic forms
No predator-prey relationships; extracellular digestion; uptake of small molecules direct from environment	Predator-prey relationships; intracellular digestion; eat other whole organisms
No cytoplasmic membrane system, ("endoplasmic reticulum"); no cytoplasmic streaming, food-vacuole formation, etc.	Extensive cytoplasmic membrane "endoplasmic reticulum" system; take in particulate food through vacuoles, cytoplasmic streaming, etc.
Examples of Prokaryote Organisms	Examples of Eukaryote Organisms
All eubacteria (desulfobacterios, <i>Escherichia coli</i> , pseudomonads, iron bacteria, bacilli, N_2 -fixing bacteria, etc.); all blue green algae; all "actinomycetous fungi" (streptomycetes, mycobacteria, etc.); spirochaetes; myxobacteria, mycoplasmas, rickettsias	All animals (sponges, comb jellies, coelenterates, brachiopods, bryozoans, annelids, enteroprotists, gastropods, arthropods, echinoderms, tunicates, fish, mammals, etc.); all "higher" algae (all algae except blue greens: red and brown sea weeds, stone-warts, diatoms, dinoflagellates, chlorellas, <i>Cyanidium</i> , etc.); all "higher" fungi (water molds, chytrids, mushrooms, yeasts, sac fungi, etc.); all green plants (mosses, liverworts, ferns, cycads, conifers, flowering plants, etc.); all protozoans, (amoebae, radiolarians, foraminiferans, ciliates, sporozoans, etc.)

SOURCE.—Modified from Stanier et al. 1963.

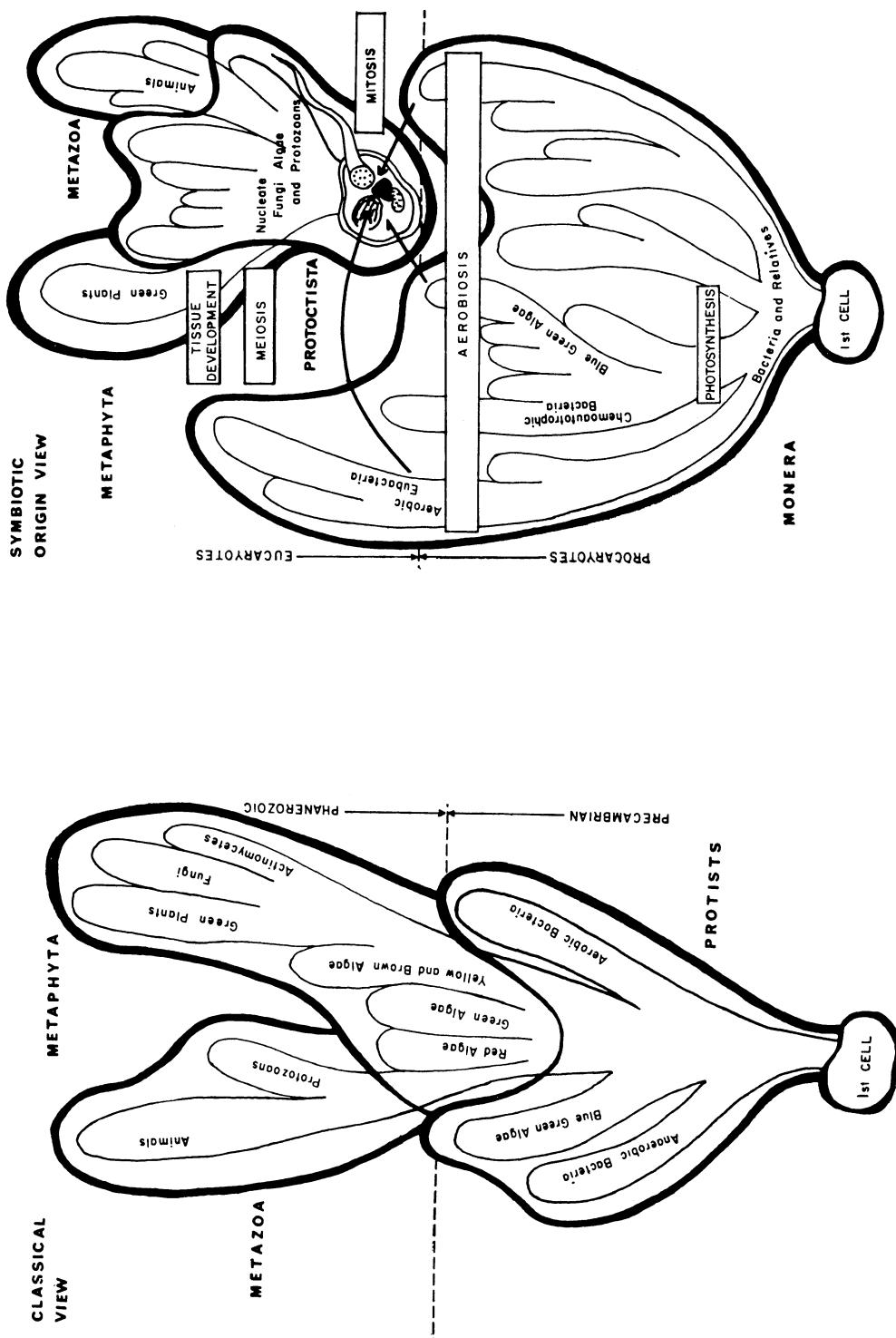


FIG. 3.—Comparison between classical (Klein and Cronquist 1967) and symbiotic (Margulis 1968) phylogenies of the lower organisms

the primitive earth by incident solar radiation (Fox 1965). In order to serve as abiotic precursors to living systems, these materials must have included a variety of amino acid and nucleic acid derivatives. However, of the innumerable possible organic compounds, only a very few are synthesized by cells. Many more organic isomers never found in living systems should have been produced abiotically. Thus, a diverse assortment of compounds, comparable to those produced under simulated primitive earth conditions, would be expected (Oró 1965, Ponnamperuma and Gabel 1968). For example, microspheres like those produced by anhydrous copolymerization of amino acids (Fox et al. 1967) containing other linkages in addition to the standard peptide ones might have been produced. It is not likely that optical activity would be present in any abiotic material (but see Fox et al. 1956), and there would be little fractionation of carbon or sulfur isotopes (Thode and Monster 1964).

II. BIOTIC ORGANIC MATTER: PROKARYOTIC CELLS

The minimal independent self-replicating unit upon which natural selection can act is a cell (fig. 4). The chemistry of protein synthesis coded for by nucleic acids is the same in all living cells. The existence of the code itself argues eloquently for the hypothetical common ancestry of extant organisms. Ever since the code was established as the basis for replication in primitive cells, all of the essential chemical components of cellular systems (fig. 4) must have been potentially fossilizable. The primary sources of energy for the first cellular systems were presumably relatively reduced abiogenic organic compounds, such as acetate, lactate, pyruvate, alanine, glycine, etc. (Oparin, Haldane, reprinted in Bernal 1967). Compounds such as these, probably produced directly by ultraviolet solar irradiation of the primitive atmosphere (Ponnamperuma and Gabel 1968), are universal metabolites in present-day living systems. Along with all the chemical requirements for replication, the earliest

cells should have contained optically active materials, for example, the d-series of carbohydrates and the l-series of amino acids, isomers most characteristic of living materials today. Since amino acid polymerization into proteins is obligatorily linked with nucleic acid polymerization in living systems (Watson, 1966), biotic peptides invariably should be associated with nucleic acids.

One of the most widespread biochemical pathways in prokaryotic organisms is CO₂ fixation (fig. 1). Atmospheric CO₂, probably available in sufficient quantity throughout geological time (Holland, 1966), was combined by microorganisms into reduced carbon very early in the Precambrian. As in extant organisms, either atmospheric hydrogen gas or organic compounds must have served as sources of hydrogen atoms for the CO₂ reduction. Enzymes and intermediates of the CO₂ fixation "dark cycle" (Bassham and Jensen 1967), such as phosphoglyceric acid, phosphoglyceraldehyde, NADP (nicotine amide adenine dinucleotide phosphate), and ribose would have been deposited in sediments when the cells died. The presence of CO₂ fixation pathways in strictly anaerobic nonphotosynthetic microbes (e.g., *Clostridium* and *Desulfovibrio*) implies that isotopic fractionation of carbon and sulfur, biological production of sulfide (H₂S) from sulfate, thiosulfate and hydrogen gas, and the deposition of biologically reduced carbon, in general preceded the origin of all photosynthetic systems.

The fixation of atmospheric nitrogen by microbial cells is also a common metabolic pathway among anaerobic, nonphotosynthetic microbes (e.g., *Clostridium*). Microbial nitrogen incorporation into organic nitrogen-containing compounds is mediated by molybdenum ferrodoxin enzyme systems (Mortenson et al. 1968). Evolution of the N₂ fixation system probably followed closely after the origin of the CO₂ fixing pathways. Evidence for both nitrogen and carbon dioxide fixations should be found in sediments laid down before photosynthetic organisms evolved.

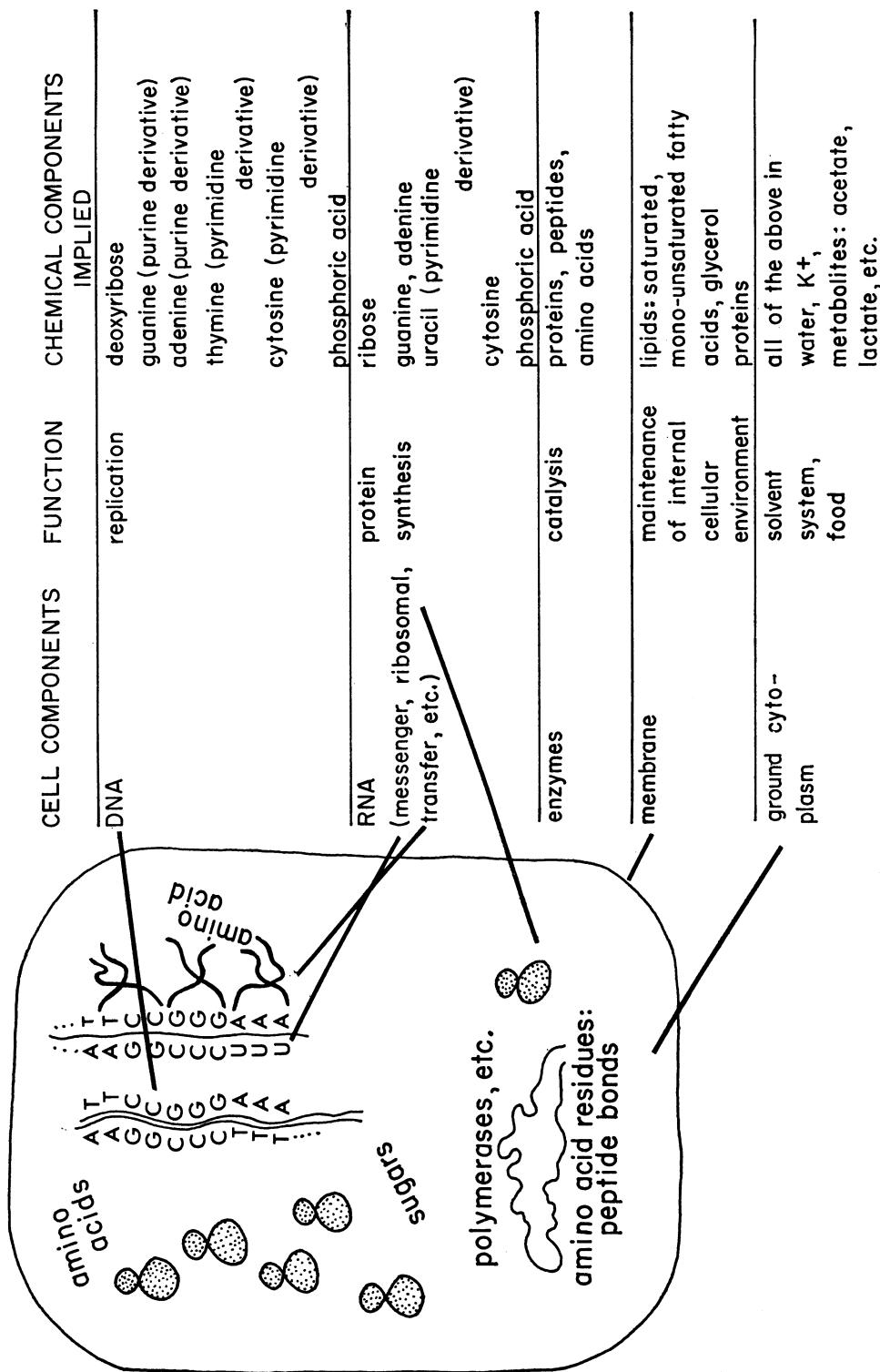


FIG. 4.—Chemistry of the minimal self-replicating unit: the cell (diagrammatic)

An early biosynthetic innovation, probably selected because it protected cells from photooxidation, was the biosynthesis of isoprene derivatives. Some examples of these are the phytol chain on chlorophylls; carotenoids, vitamin A, squalene, and phycoobilin. Isoprene derivatives are produced biosynthetically from acetate. Although most organisms contain isoprene derivatives, this class of compounds is always associated with photosynthetic systems, including strictly anaerobic bacterial photosyntheses.

Closely parallel to the evolution of the biosynthesis of isoprene derivatives came a major evolutionary development in microbes, one which eventually led to standard "green plant-type" photosynthetic organisms: the biosynthesis of porphyrin derivatives. These metal-chelated tetrapyrroles are found today in nearly all prokaryotic microbes. They are produced biosynthetically from δ -amino-levulinic acid, a compound derived from acetate and glycine. Porphyrin derivatives such as iron containing coenzymes (e.g., those in catalase, peroxidase, and cytochrome), the magnesium-chelated chlorophylls, and the cobalt-chelated vitamin B_{12} should have been deposited by microbial photosynthesizers before any oxygen-eliminating photoautotrophs evolved. The lack of porphyrins of any kind in many prokaryotic heterotrophs (e.g., some clostridia and the presence of porphyrins in their presumed relatives (e.g., some bacilli) imply that the porphyrin-synthesizing pathways evolved inside cells. Although porphyrin (as well as many other organic compounds) is yielded in small quantities in experiments simulating primitive earth conditions (Hodgson and Ponnamperuma 1968), the deposition of most specifically identifiable porphyrin derivatives was probably biogenic.

All of the above biosynthetic capabilities in microbes must have preceded the evolution of microbial photosynthesis. The primitive bacterial photosynthesizers (as opposed to the oxygen-eliminating photosynthesis of green plants and blue green algae) presum-

ably were the first photoautotrophs. Bacterial photosynthesis results in the formation of organic carbon; in many microbes, elemental sulfur or sulfates may be deposited as well. Gaseous oxygen is never produced as a by-product in this type of photosynthesis.

Only after the evolution of cellular systems resulting in the synthesis of the organic materials discussed above could oxygen-eliminating photosynthesis have evolved. However, there is little doubt that "green plant-type" photosynthesis arose in prokaryotic cells, ancestors of present-day blue green algae (Echlin and Morris 1965), and not in higher plant cells. Microfossils which have been identified as blue green algae are found in cherts of the Gunflint Iron Formation (Barghoorn and Tyler 1965); therefore, the biological potential for atmospheric oxygen production must have been present at least 1.6–2 billion years ago. The older Bulawayan stromatolites (2.7 billion years) as well as those from the Great Slave Lake (2 billion years, P. Hoffman, oral communication 1968) were also probably formed by blue green algae.

Many prokaryotes are obligate aerobes that only survive under conditions of low oxygen tension. Studies of the metabolism of prokaryotic microbes strongly suggest that the entire group evolved in response to progressively increasing amounts of atmospheric oxygen. Many genera contain members that utilize oxygen when it is available but can utilize nitrogen instead under anaerobic conditions (fig. 1; Prevot, 1966). There is some evidence that the iron bacteria, which are normally aerobic, may be able to grow entirely on mineral media containing hydrated $FeCO_3$ and CO_2 . Microfossils morphologically similar to certain modern iron bacteria are known from the Gunflint cherts (Schopf et al. 1965); perhaps the Banded Iron Formations are related to microbial activity (Cloud 1968).

Other biosyntheses characteristic of the prokaryotic group include the formation of cell wall components such as diaminopimelic acid and glucosamine, pectins (d-galac-

turonic acid polymers), celluloses (d-glucopyranose polymers), and glycogen. Certainly, by the time blue green algae had evolved (but before any animals or eukaryotic plants appeared), there was biosynthetic production of such polymeric carbohydrates, aliphatic organic acids, and a multitude of other compounds characteristic of prokaryotes. Traces of these may have been deposited in Precambrian sediments. A biochemical innovation which may have accompanied the appearance of aerobically respiring blue green algae was the synthesis of polyunsaturated hydrocarbons (Holton et al. 1968) and perhaps even certain steroids (De Souza and Nes, 1968).

III. BIOTIC ORGANIC MATTER: EUKARYOTIC CELLS

According to the symbiotic theory, all eukaryotic cells arose (from the geological point of view) at the same time. Although the first mitotic-meiotic eukaryotic cells may have taken a billion years to evolve from amoeboflagellated ancestors, once mitosis and meiosis were established, tissue and organ development characteristic of eukaryotes followed soon after. The phylogeny of eukaryotes (fig. 2) is based on the assumption that these organisms arose during the evolution of eukaryote mitosis. The appearance of all the major eukaryotic plant and animal phyla occurred after a significant accumulation of gaseous oxygen in the atmosphere, because all eukaryotic metabolism is fundamentally aerobic. The synthesis and diversification of sterols and steroids (sterane derivatives) paralleled the evolution of higher cells. These complex molecules, which involve molecular oxygen in their biosynthesis, are ubiquitously distributed in higher plant and animal tissues. Polyunsaturated hydrocarbons, such as linoleic and linolenic acids (Olson 1966), are characteristically produced and required by aerobic eukaryotes. Thus the presence of certain steroids and polyunsaturated fatty acids in sediments might be good geochemical indicators for the presence of aerobic, eukaryotic organisms. On these grounds it is

possible to question the interpretation of the discovery of sterane in early Precambrian sediments (Burlingame et al. 1965).

IV. BIOTIC ORGANIC MATTER: EUKARYOTIC MULTICELLULAR ORGANISMS

The record of organic evolution from the base of the Cambrian to the present consists of micro- and macrofossil forms, nearly all with indisputable affinities to extant organisms. Specific organic syntheses characteristic of these higher groups (e.g., some of the alkaloids of green plants), possibly detectable by the newer techniques of organic geochemistry, might clarify evolutionary relationships between extant and fossil forms. For example, it is known that a major class of colored compounds (the flavonoids, e.g., anthocyanin) are produced only by vascular plants. It is likely that the end products of other metabolic pathways in higher plants and animals will also be correlated with both a specific line of organisms and a significant source of selection pressure in the natural environment.

Table 2 summarizes these remarks on the innovative biosynthetic pathways in major groups of organisms. The entries are ordered chronologically; tentative dates have been assigned for the sole purpose of orientation. Since potentialities to form a general class of organic compounds, once evolved, seem to persist indefinitely, any sediment at any later time should contain geologically stable derivatives of all the materials that originated below it. If eukaryotes arose by serial symbioses, a discontinuity is expected between the first seven entries and the last four. The former should be associate with prokaryotic microfossil remains, and the last four with fossils of eukaryotic organisms.

It has been argued that each of the major products of these long biosynthetic pathways (i.e., some of the entries in table 2) may have conferred the following selective advantages on organisms: nucleic acid and protein synthesis insure efficient reproduction (Rich 1962); porphyrins and isoprenes protect against oxygen, especially in light

(Krinsky 1966); chlorophylls and carotenoids provide for the photoproduction of adenosine triphosphate (ATP); steroids and sterols, originally involved in the production of intracellular membranes leading to the formation of food vacuoles and effective predation, were differentiated for many dif-

ferent types of sexual dimorphisms; flavonoids were selected to insure outbreeding in plants.

This type of evolutionary explanation of biochemical diversity is analogous to explanations of the evolution of both terrestrial vertebrates and terrestrial green plants

TABLE 2

DEPOSITION OF ORGANIC MATERIALS IN SEDIMENTS: ORDER PREDICTED BY SYMBIOTIC THEORY

Approx. Time of Evolution of ($\times 10^9$ yrs) Group of Organisms	Most Primitive Groups in Which Synthetic Pathway First Appears	Correlated Synthetic Pathways	Potential Sedimentary Evidence
Precambrian: 4.5-3.0.....	None	Abiogenic organic matter, lack of optical activity, wide varieties of isomers
3.5-2.0.....	First anaerobic cellular organisms	Optical activity, nucleic acid replicatory system (fig. 4), membranes	Optical activity, nucleic acid and protein derivatives, organic phosphorus, lipid derivatives: mono- or bi-saturated fatty acids, carbon and sulfur isotope fractionation, microfossils
3.5-2.0.....	Anaerobic fermenters	CO_2 fixation (using H_2 or organic hydrogen to reduce CO_2)	Reduced carbon compounds, sulfide deposition, intermediates in CO_2 reduction pathways, molybdo-ferredoxin
3.5-2.0.....	Anaerobic bacterial photosynthesizers	Carotenoids, bacterial chlorophylls	Porphyrin and isoprene derivatives, organic carbon, sulfate, sulfur
3.0-1.5.....	Anaerobic respirers	Cytochromes, catalase, cobalamin (vitamin B_{12})	Porphyrin, isoprene derivatives
3.0-1.5.....	Blue green algae	O_2 -eliminating photosynthesis, chlorophyll a	Some oxidized sediments, some polyunsaturated fatty acids and steroids
2.5-0.5.....	Aerobic prokaryotes	Iron, sulfur and nitrogen oxidations	Iron and manganese oxides, nitrates, diaminopimelic acid, pectin, cellulose, glycogen, muramic acid, etc.
Phanerozoic: 1.0-0.5.....	Eukaryote cells	Steroids, sterols, polyunsaturated hydrocarbons, microtubular mitotic and flagellar proteins	Sterol derivatives, polyunsaturated hydrocarbon derivatives
1.0-0.5.....	Eukaryotic fungi	Quinonoids	Derivatives of radicinin, citrinin, citromycin, fulvic acid, penicillins, etc.
0.6-0.3.....	Vascular green plants	Flavonoids, lignin, some alkaloids	Flavonoid derivatives, more O_2 eliminated, some alkaloids
0.6-0.3.....	Lichens	"Lichenic acids"; depsides, depsidones, dibenzofurans	Depside derivatives, etc.

and fungi in the Paleozoic. Morphological variations are interpreted as part of a large series of evolutionary adaptations to the selection pressure of the dry, nonbuoyant conditions on the land. In this connection there is no real biological evidence for the suggestion of Berkner and Marshall (1965) that protection from ultraviolet light was ever a significant selective factor in the Phanerozoic environment.

The rapidly accumulating data on organic materials in sediments must be consulted in order to assess the validity of the view presented here. The discoveries of Precambrian microfossils by Barghoorn and Schopf (1966) and Cloud (1968) certainly

seem consistent. It is becoming more apparent that the geological record must be consulted for direct evidence of the paths of evolution even in microbes.

ACKNOWLEDGMENTS.—Professors E. S. Barghoorn, J. Wm. Schopf, P. E. Cloud, Jr., G. E. Hutchinson, H. D. Holland, A. L. Fischer, A. R. Palmer, and R. Siever have all been immeasurably helpful in introducing me to the little I know about geology. I also thank Professors B. Nagy, R. A. Lewin, G. E. Hutchinson, and my Boston University colleagues, Professors R. E. Estes and B. Cameron, for invaluable criticism of the manuscript. The support of the Boston University Graduate School and the National Science Foundation are also gratefully acknowledged.

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